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Grant Proposal

Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity-ecosystem functioning relationships

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Abstract

The functioning and service provisioning of ecosystems in the face of anthropogenic environmental and biodiversity change is a cornerstone of ecological research. The last three decades of biodiversity–ecosystem functioning (BEF) research have provided compelling evidence for the significant positive role of biodiversity in the functioning of many ecosystems. Despite broad consensus of this relationship, the underlying ecological and evolutionary mechanisms have not been well understood. This complicates the transition from a description of patterns to a predictive science. The proposed Research Unit aims at filling this gap of knowledge by applying novel experimental and analytical approaches in one of the longest-running biodiversity experiments in the world: the Jena Experiment. The central aim of the Research Unit is to uncover the mechanisms that determine BEF relationships in the short- and in the long-term. Increasing BEF relationships with time in long-term experiments do not only call for a paradigm shift in the appreciation of the relevance of biodiversity change, they likely are key to understanding the mechanisms of BEF relationships in general. The subprojects of the proposed Research Unit fall into two tightly linked main categories with two research areas each that aim at exploring variation in community assembly processes and resulting differences in biotic interactions as determinants of the long-term BEF relationship. Subprojects under “Microbial community assembly” and “Assembly and functions of animal communities” mostly focus on plant diversity effects on the assembly of communities and their feedback effects on biotic interactions and ecosystem functions. Subprojects under “Mediators of plant-biotic interactions” and “Intraspecific diversity and micro-evolutionary changes” mostly focus on plant diversity effects on plant trait expression and micro-evolutionary adaptation, and subsequent feedback effects on biotic interactions and ecosystem functions. This unification of evolutionary and ecosystem processes requires collaboration across the proposed subprojects in targeted plant and soil history experiments using cutting-edge technology and will produce significant synergies and novel mechanistic insights into BEF relationships. The Research Unit of the Jena Experiment is uniquely positioned in this context by taking an interdisciplinary and integrative approach to capture whole-ecosystem responses to changes in biodiversity and to advance a vibrant research field.

Keywords

Biodiversity loss, biodiversity-ecosystem functioning, ecosystem services, plant-soil feedback effects, grassland

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State of the art and preliminary work

Temporal changes of biodiversity effects on ecosystem functions

A plethora of experimental studies has shown that the magnitude and stability of ecosystem functions increase with biodiversity (Cardinale et al. 2012, Isbell et al. 2015). Short-term experiments mostly predict a saturating relationship between biodiversity and ecosystem functions, implying that biodiversity effects are stronger at low biodiversity, and the loss of species at higher biodiversity levels has little effect (Cardinale et al. 2011, Cardinale et al. 2012). However, the few existing long-term experiments have challenged this view by demonstrating ***the strength of the biodiversity effect to increase with time,*** **i.e.,** ***the saturating BEF relationship to become (more) linear*** (Reich et al. 2012, Guerrero-Ramírez et al. 2017). In fact, biodiversity effects seem to become increasingly important when more environmental contexts, functions, and experimental years are considered (Isbell et al. 2011, Eisenhauer et al. 2018 These findings contrast with the notion of saturating biodiversity effects, and thus have fundamentally different implications for the consequences of biodiversity change as well as the many related functions and services for humankind. Long-term biodiversity experiments are, therefore, not only key to understand mechanisms underlying BEF relationships at ecological equilibrium (Eisenhauer et al. 2012a, Eisenhauer et al. 2012b), but also to provide better-informed recommendations for land managers and policy makers (Hungate et al. 2017, Isbell et al. 2017). ***The Jena Experiment is one of the few existing long-term experiments that allows scientists to assess whether short-term and long-term biodiversity effects are indeed qualitatively different and to uncover the mechanistic basis of divergence of short- versus long-term effects.***

While the diverging trends are apparent, it is currently ***unclear whether strengthening biodiversity effects are attributable to***

1. ***deteriorating performance of low diversity communities***,
2. ***improving performance of high diversity communities, or***
3. ***both*** (Meyer et al. 2016, Guerrero-Ramírez et al. 2017, Eisenhauer et al. 2012b).

Since low-diversity plant communities are widely used in landscapes managed for production, such as agricultural systems and tree plantations (Isbell et al. 2017), deteriorating low-diversity communities over time may have important implications for the long-term provisioning of vital ecosystem services in managed ecosystems. A recent meta-analysis of 26 long-term grassland and forest biodiversity experiments shows that biodiversity–ecosystem functioning relationships strengthen mainly by greater increases in functioning in high-diversity communities in grasslands and forests (Guerrero-Ramírez et al. 2017). In grasslands, however, biodiversity effects also strengthen due to decreases in functioning in low-diversity communities. The synthesis of multiple ecosystem functions in the Jena Experiment also suggests that both deteriorating performance at low diversity and improving performance at high diversity contribute to strengthening BEF relationships over time (Meyer et al. 2016). The generality of those findings and the paucity of experiments that capture long-term effects puts long-term studies in the unique position to unravel the mechanisms that are responsible for increasing biodiversity effects over time (Eisenhauer 2018). Moreover, in order to derive such a mechanistic understanding, potential confounding influences of calendar year have to be ruled out by comparing ecosystems of different age in the same calendar years, as we do in the Field Experiment that we set up in preparation of the requested Research Unit (see below). ***Thus, the Jena Experiment in particular allows in-depth understanding of the full range of biotic interactions and eco-evolutionary dynamics and how they interactively influence ecosystem functioning in the short- and in the long-term.***

Potential mechanisms underlying temporal changes of biodiversity effects

There are several possible causes that may explain the declining performance of low-diversity plant communities over time. Many of those are related to the ***assembly of plant community-specific above- and belowground microbial and animal communities*** (Lange et al. 2015, Ebeling et al. 2018, Schmid et al. 2019, Schuldt et al. 2019) that feed back to plant community composition and performance through different biotic interactions (Bever et al. 1997, Bever 2003, Eisenhauer 2012). Accumulation of specific plant antagonists and imbalanced use of resources can generate '*negative feedback effects*' on plants at low plant diversity (Schnitzer et al. 2011, Eisenhauer et al. 2012a, Kulmatiski et al. 2012, Mommer et al. 2018). On the other side of the spectrum, improving high-diversity communities have been associated with diversity-dependent increases in soil fertility from greater storage of carbon and nitrogen (Fornara and Tilman 2008, Reich et al. 2012, Leimer et al. 2016), increase in plant complementarity effects (Cardinale et al. 2007, Marquard et al. 2009, Reich et al. 2012), accumulation of plant growth facilitators at high plant diversity ('*positive feedback effects*' by *e.g.*, mycorrhizal fungi, biocontrol bacteria; Eisenhauer et al. 2012a, Latz et al. 2012), and, more recently, increasing niche differentiation by co-evolutionary adaptation (Zuppinger-Dingley et al. 2014). Both types of feedback effects may ultimately co-determine an increase in the strength of positive plant diversity effects in the long term (Eisenhauer 2012, Eisenhauer 2018). ***However, the relative importance of positive and negative feedbacks as well as the main agents of varying community assembly effects, their eco-evolutionary implications, and their context-dependency remain poorly understood.***

Ecological processes, such as changes in the competitive environment as well as antagonistic and beneficial multitrophic interaction partners above and below the ground impose selective pressures on members of the community and thereby create ‘eco-to-evo’ feedbacks (Hendry 2016). The subsequent evolutionary changes, in turn, will alter the conditions for other members of the community *via* ‘evo-to-eco’ feedbacks (Whitham et al. 2006, Lipowsky et al. 2011, van Moorsel et al. 2018), giving rise to complex eco-evolutionary dynamics (**Fig. 1**). Some changes in plant traits will be plastic responses, while others are genetic or epigenetic in origin, and lead to adaptation and differences along the diversity gradient (Whitham et al. 2006, Lipowsky et al. 2011, van Moorsel et al. 2018). Understanding the relative role of these components is of importance, because the mechanisms determine how reversible the changes are and how much they contribute to long-term BEF relationships. ***Open-ended questions are if variation in trait expression is related to micro-evolutionary changes as well as the role of traits that may be relevant for biotic interactions and feedback effects, such as defense traits at the physiological level.*** Evolutionary changes, such as increased niche differentiation (Zuppinger-Dingley et al. 2014), and increased resource-use complementarity due to community assembly processes (Reich et al. 2012, Roscher et al. 2013), will slowly build up and can thus produce increasing biodiversity effects over time (Fig. 1). Yet, it remains unexplored whether short-term and long-term biodiversity effects are qualitatively different, such that short-term effects may be dominated by phenotypic plasticity and community assembly, while long-term effects may be co-determined by eco-evolutionary dynamics that may continue to produce divergence in plant community performance in the long-term. ***Ultimately, ecological and evolutionary processes are intertwined, and long-term experiments are needed not only to gain basic understanding of the relative importance as well as interactions of these processes, but also to apply these concepts to better provisioning of ecosystem functions and stability*** (Tilman and Snell-Rood 2014).

The proposed Research Unit will address this knowledge gap by asking the overarching question: ***Are increasing biodiversity–ecosystem functioning relationships with time caused by changing biotic interactions due to the interplay between multitrophic community assembly processes and eco-evolutionary dynamics***? As community assembly, biotic interactions, and eco-evolutionary processes strongly interact in influencing plant traits and signals in space and time, collaboration across the proposed subprojects in targeted and unique plant history and soil history experiments using cutting-edge technology will produce significant synergies and novel mechanistic insights into BEF relationships.

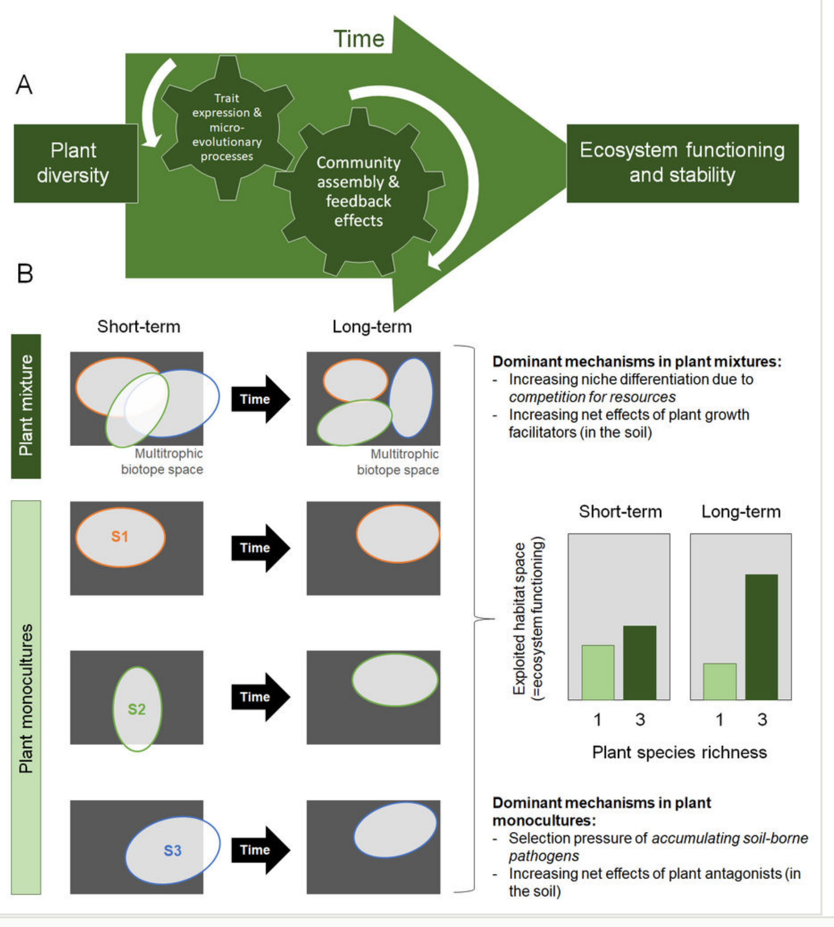

Figure 1. doi

A. Conceptual diagram of the mechanistic approach of the planned Research Unit. **B.** Conceptual scheme of the proposed evolutionary niche shifts in plant monocultures and mixtures. This idea feeds into our understanding of how evolutionary history influences the ecological interactions of species that compete for growth factors, ultimately defining biotope space (gray rectangle; Hutchinson 1978). Graphically depicted, species (ellipses) in mixture will show increasing niche differentiation over time due to competition (niche overlap). Thus, history of selection in diverse communities is expected to result in greater interspecific differences (less overlap of ellipses) and more specialization (smaller ellipses) than a history of isolation (monocultures). In monocultures, species will experience strong selection pressure by accumulating soil-borne pathogens, and species may invest energy in chemical and morphological defense traits (depicted by ellipses shifting towards the same corner of the habitat space). Plants in mixtures together may exploit more available biotope space than single monocultures, causing increasing diversity effects on ecosystem functions over time. However, there is limited support for this assumption for traits related to light (e.g., Lipowsky et al. 2015, Roscher et al. 2015) and resource use (Jesch et al. 2018) so far.

Project-related publications

Spokesperson and principle investigators highlighted.

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Objectives, concept and approach

New objectives based on a strong research history

The previous Research Units within the Jena Experiment have yielded unique insights into the role of plant diversity for multiple ecosystem functions and trophic levels (*e.g.*, Scherber et al. 2010, Allan et al. 2013, Lange et al. 2015, Lefcheck et al. 2015, Schuldt et al. 2019), stability of ecosystem functions (*e.g.*, Isbell et al. 2015, Wright et al. 2015, Craven et al. 2018), as well as first insights into the role of eco-evolutionary dynamics (*e.g.*, Zuppinger-Dingley et al. 2014, Zuppinger-Dingley et al. 2016, van Moorsel et al. 2018). However, our understanding of the ecological mechanisms (Laforest-Lapointe et al. 2017, Guerrero-Ramírez et al. 2017) and eco-evolutionary feedbacks (van Moorsel et al. 2018, Schmid et al. 2019) underlying changes in BEF relationships over time is still in its infancy. Considering multitrophic community assembly and exploring subsequent biotic interaction variation as determinant of long-term BEF relationships will be key to advance this field of research (Hines et al. 2015, Barnes et al. 2018). Specifically, ***the combination of the unique research infrastructure of the Jena Experiment and novel experimental approaches with cutting-edge technology in microbiology, chemical ecology, proximal sensing, genomics, and food web modelling will allow the proposed Research Unit to take a leading role in BEF research. We propose to zoom in on the underlying mechanisms of long-term BEF by investigating the different influences that plants experience in their interactions with plant and consumer communities.***

The subprojects (SPs) of the proposed Research Unit fall into two main categories and four tightly linked research areas (RA) (Fig. 2). Subprojects under "***Microbial community assembly***" (RA1) and "***Assembly and functions of animal communities***" (RA2) mostly focus on plant diversity effects on the assembly of consumer communities and subsequent feedback effects on plant and consumer communities and ecosystem functions. Resulting biotic interactions drive the expression of growth and defense traits, as well as micro-evolutionary processes. Thus, subprojects under "***Mediators of plant-biotic interactions***" (RA3) and "***Intraspecific diversity and micro-evolutionary changes***" (RA4) mostly focus on plant diversity effects on plant trait expression and micro-evolutionary adaptation, how this is fueled by phenotypic plasticity, genetic and/or epigenetic differentiation, and how this influences ecosystem functions. In RA1, the assembly of plant and soil microbiomes will be explored because of their crucial role as part of the plant's extended phenotype (Schnitzer et al. 2011, Laforest-Lapointe et al. 2017, Schmid et al. 2019). In RA2, taking a multitrophic perspective on BEF (Hines et al. 2015, Soliveres et al. 2016, Barnes et al. 2018), above- and belowground animal community assembly and activity patterns (Eisenhauer et al. 2018a) as well as their feedback effects on plants and ecosystem functions will be studied. In RA3, the mechanisms behind plant responses to and effects on biotic interactions and complex food webs will be studied by focusing on plant growth and defense traits and the chemical signaling with interaction partners above and below the ground with their knock-on effects on higher trophic levels. In RA4, trait changes, micro-evolutionary adaptation, and population genetics will be investigated by studying the intraspecific diversity of plant communities. As a consortium, we will thus be able to study the assembly of above-belowground communities and subsequent feedback effects, as well as plant trait expression and micro-evolutionary processes. Notably, ***these two main categories are closely linked as plastic micro-evolutionary responses of plants are supposed to be strongly influenced by above-belowground community assembly and their feedback effects, and*** **vice versa** (Fig. 1). These conceptual links are exemplified by the many collaborations of subprojects across categories and research fields (Fig. 2).

All of the proposed subprojects will utilize common experimental setups that explore the eco-evolutionary history of plant and soil communities. ***Community-level studies*** will explore BEF relationships as affected by plant history and/or soil history. Plant history refers to the abiotic and biotic selection pressures that plants have experienced in their respective communities since the start of the Jena Experiment, while soil history encompasses abiotic and biotic soil properties that have emerged from plant-soil interactions (Bever 2003, Schmid et al. 2019). ***Plant individual-specific studies*** will advance the mechanistic understanding of community-level responses and processes by exploring plants' investments into growth and/or defense, interactions with microorganisms and animals above and below the ground, and how plant diversity-induced alterations in genetic diversity and trait expression change the performance of the plants and the interactions with their abiotic and biotic environment.

Novel tools to study temporal changes in biotic interactions and BEF effects

The exploration of biotic interactions within and across trophic levels is one key research frontier to mechanistically understand BEF relationships (Ives et al. 2005, Thébault and Loreau 2006, Thompson et al. 2012, Hines et al. 2015, Barnes et al. 2018). Although this research direction has been advocated for more than a decade, it is only now that we have the appropriate tools in hand to explore biotic interactions in more complexity. Recent progress in molecular and proximal sensing techniques now allow scientists to identify and quantify the microbial players in plants' aboveground-belowground interactions (*e.g.*, Laforest-Lapointe et al. 2017, Schmid et al. 2019) as well as to explore the temporal dynamics of biotic interactions (*e.g.*, Dell et al. 2014, Eisenhauer et al. 2018a, Schuldt et al. 2019). At the same time, molecular sequencing techniques have been refined, such as cost-effective exploration and comparative analysis of DNA methylation and genetic variation in hundreds of samples *de novo* (van Gurp et al. 2016), and network analyses have emerged as tools to identify hub taxa and community-wide shifts in plant-microbe interactions (*e.g.*, Morriën et al. 2017) as well as energy fluxes through food webs (Schwarz et al. 2017, Barnes et al. 2018). These novel methods allow us to characterize plant history and soil history effects on aboveground-belowground interactions, phenotypic and molecular adaptations (Berg and Coop 2014), and the distribution and maintenance of standing genetic variation (Vellend et al. 2014). Furthermore, we are now able to explore the chemical communication of plants above- and belowground determining interactions with mutualists and antagonists (van Dam and Bouwmeester 2016).

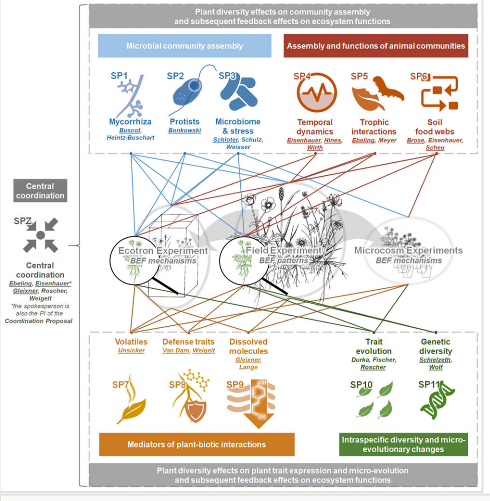

Figure 2. doi

Structure of the proposed Research Unit. Three complementary experimental approaches are envisaged to study long-term biodiversity-ecosystem function (BEF) relationships, and how these are influenced by plant history and soil history. BEF patterns are studied in the Field Experiment with long-term plant diversity plots and manipulations of soil-history effects. BEF mechanisms are studied in the Ecotron Experiment and in Microcosm Experiments. In the Ecotron Experiment, plant history and soil history are independently crossed and detailed process measurements are possible. The Microcosm Experiments zoom in on focal interactions. In the Field Experiment and in the Ecotron Experiment, studies are conducted at the community level as well as at the plant individual level (magnifier; see detailed design of studies in the Appendices). Subprojects' (SPs') participation in experiments are illustrated with lines. The SPs of the proposed Research Unit fall into two tightly linked main categories (in gray) with two research areas each that aim at exploring variation in community assembly processes, micro-evolutionary changes, and resulting differences in biotic interactions as determinants of the long-term BEF relationship. Subprojects under "Microbial community assembly" (blue) and "Assembly and functions of animal communities" (red) mostly focus on plant diversity effects on the assembly of communities and their feedback effects on biotic interactions and ecosystem functions, while subprojects under "Mediators of plant-biotic interactions" (orange) and "Intraspecific diversity and micro-evolutionary changes" (green) mostly focus on plant diversity effects on plant trait expression and micro-evolution. PIs with requested personnel are underlined.

Notably, ***addressing the main objectives of the proposed Research Unit with these novel techniques requires a stepwise approach***. In the proposed first phase of the Research Unit, we plan to build on recently established (Field Experiment; see below) and envisaged experiments (Ecotron Experiment and Microcosm Experiments; see below and individual SP's proposals, respectively) to study the effects of plant history and soil history on BEF relationships and to separate those from potentially confounding climate effects. These experiments have sophisticated designs and provide the unique framework to describe microbial and animal community assembly patterns, morphological and chemical mediators of plant-biotic interactions, intraspecific plant diversity and micro-evolutionary changes, as well as the linkages to ecosystem functioning. ***Many novel tools will for the first time be employed in a BEF context and will thus contribute to describing new BEF patterns and develop hypotheses inspiring future experimental work that will build the basis for the second phase of the proposed Research Unit***. For instance, the detailed investigation of microbial communities, comprising plant antagonists and mutualists, is an important first step to identify and cultivate potential key taxa that may then be manipulated in future experiments in the second phase. Similarly, the identification of important chemical traits and signals in the first phase of the Research Unit could allow us testing their role in biotic interactions and BEF relationships by targeted manipulations and/or lab experiments. The exploration of energy fluxes through food webs may enable us to detect key nodes that could be manipulated in subsequent experiments. Moreover, the discovery of key biological activity periods may guide the timing of future sampling campaigns. Taken together, we see the proposed research in the first phase of the Research Units as the prerequisite for future mechanistic studies, an approach that is already exemplified by the Microcosm Experiments.

Complementary expertise facilitates the "Research Unit's functioning"

The previous Research Units in the framework of the Jena Experiment have had a unique role in BEF research by exploring whole-ecosystem responses to changes in biodiversity. Thus, the Jena Experiment is internationally widely known and respected as a key pillar in BEF research as well as one of the few running long-term biodiversity experiments in grassland. The proposed Research Unit will build on the unique strengths of the Jena Experiment, yet taking a novel approach in studying BEF relationships. ***The interdisciplinary approach (collaboration between animal ecologists, biochemists, plant ecologists, soil ecologists, soil microbiologists, evolutionary ecologists, and food web modelers) is highly innovative and world-leading.*** In order to address some of the most pressing challenges in BEF research, novel experimental, theoretical, and analytical approaches, expertise, and a completely realigned group of PIs is necessary. The consortium for the proposed Research Unit comprises scientists that were already involved in earlier phases of the Jena Experiment and many new ones that were selected in the past years to bring new expertise into the group, in particular in chemical ecology, soil microbiology, proximate sensing, evolutionary ecology, and ecological modeling. A particular strength of the consortium is a very close cooperation among the different subprojects (Fig. 2). This collaboration is indicated by collaborative work in the two main experiments, complementary analyses on the same plant individuals, and joint sampling campaigns. The proposed Research Unit includes scientists and collaborators from various universities and research institutes in Germany and Switzerland. German participation includes the universities of Göttingen, Halle, Jena, Köln, Leipzig, Frankfurt, TU and LMU Munich, the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, the Max Planck Institutes for Biogeochemistry and Chemical Ecology (both in Jena), as well as the Helmholtz-Centres for Environmental Research in Halle/Leipzig and for Health and Environment Munich, and we propose to strengthen this team through close collaborations with ***Mercator Fellows*** (Prof. Dr. Jeannine Cavender-Bares, Prof. Dr. Forest Isbell, Prof. Dr. Liesje Mommer, Prof Dr. Kevin Mueller) that will complement our expertise and connect us with international scientists and experimental infrastructures.

Joint work programme including proposed research methods

Cutting-edge techniques meet novel experimental approaches

We propose to use a set of three complementary experimental approaches (see Table 1 for the core experimental infrastructures) to advance the mechanistic understanding of BEF relationships by focusing on trait variation and biotic interaction variation caused by multitrophic community assembly as well as eco-evolutionary feedbacks as determinants of long-term plant diversity effects on ecosystem functioning (Fig. 1). While the ***Field Experiment*** allows to test important patterns in BEF relationships and the role of soil history, the ***Ecotron Experiment*** and ***Microcosm Experiments*** enable zooming in on the underlying mechanisms and to study effects of plant history and soil history (Fig. 2). ***The unifying rationale of the planned Research Unit is that plant interactions and interactions of plants with higher trophic levels (including microorganisms and animals) determine phenotypic plasticity and micro-evolutionary processes that together trigger ecosystem functioning.*** The planned Research Unit will embrace this plasticity of traits and their multitrophic interaction environment as well as their long-term evolutionary changes. In all experimental approaches, studying plant and soil eco-evolutionary history effects and their interactions will be the main ingredients to better understand why diverse plant communities function better than low-diversity plant communities and why this difference increases over time (Reich et al. 2012, Guerrero-Ramírez et al. 2017).

Table 1.

Unique features of the **Field Experiment** and the **Ecotron Experiment** that will build the core experimental infrastructures of the proposed Research Unit. The complementary Microcosm Experiments are explained in the respective subprojects' proposals (not shown here).

Field Experiment	**Ecotron Experiment**
• *Study of **biodiversity-ecosystem function patterns***	• *Study of **biodiversity-ecosystem function mechanisms***
• Long-term **soil history** effects (17 years)	• Orthogonal cross of **soil history** and **plant history** treatments

Field Experiment	Ecotron Experiment
• **Random species compositions** for species-independent conclusions	• Possibility to study **species-specific effects** and two-species interactions along the plant diversity gradient
• **Realistic field conditions** and separation of community age from time effects	• **Controlled environmental conditions** for detailed process and behavioral measurements
• Age-structured communities	• Plant individuals of the same age/development stage
• Plant diversity levels: 1, 2, 4, 8, 16, 60	• Plant diversity levels: 1, 2, 3, 6
• Plant species richness and plant functional group effects	• Plant species richness and dissimilarity effects in temporal resource use
• Large, undisturbed plots allowing for **repeated measurements** of many subprojects and the continuation of **unique time series**	• Intact soil monoliths in lysimeters with the respective soil communities that can be **destructively harvested**
• Biodiversity-induced **variations in plant density**	• **Equal plant densities** across plant diversity levels and limited weeding effects

In the ***Field Experiment*** (for hypotheses see Fig. 3; Vogel et al. 2019; **Suppl. materials 1, 2**) long-term soil history effects can be studied under field conditions, where random combinations of plant species from a large species pool (**Table 1**; Suppl. material 3) form the longest running plant diversity gradient in the world (Lefcheck et al. 2015). In the iDiv Ecotron (***Ecotron Experiment***; **Suppl. materials 4, 5**), intact soil monoliths can be studied, environmental conditions and plant density can be controlled, plants with different community histories (*i.e.*, community-selected plants) can be crossed with soils that have different histories, and individual plant species that differ in temporal resource use traits can be followed through the diversity gradient (Table 1). In the Ecotron Experiment (Fig. 4; Suppl. material 4), plant communities are proposed to be planted in equal densities, and weeding disturbances will not co-vary with the plant diversity gradient, addressing some concerns expressed regarding BEF studies in grasslands (Weisser et al. 2017). The controlled Ecotron environment will allow to study species interactions and perform sophisticated process measurements that currently are impossible under field conditions. Further ***Microcosm Experiments*** will focus on isolating mechanisms underlying focal interactions. While all planned subprojects will work in the Field Experiment and Ecotron Experiment, allowing for collaborations and synergies among subprojects, Microcosm Experiments will have more subproject-specific foci (Fig. 2). Common phytometer species and plant species-specific analyses will further link the research activities of all subprojects across experimental set-ups (Fig. 2).

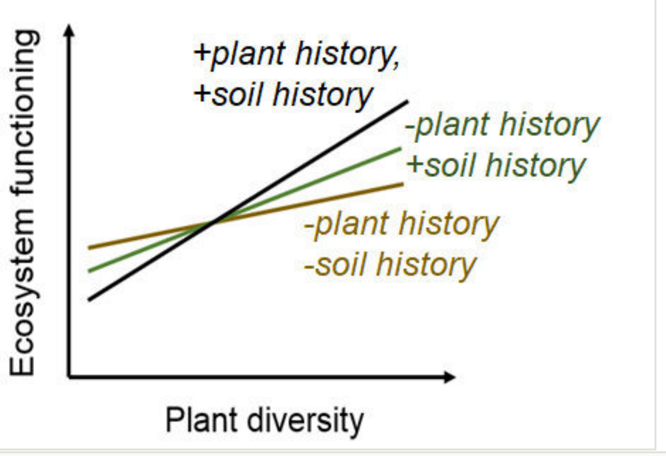

Figure 3. doi

Hypothesized slope of BEF relationships in the different treatments of the Field Experiment (see main text for details). Note that the 'with plant history, with soil history' only serves as a control in the Field Experiment, and effects of plant history can only be tested in the planned Ecotron Experiment. Redrawn after Vogel et al. (2019). '+', with; '-', without.

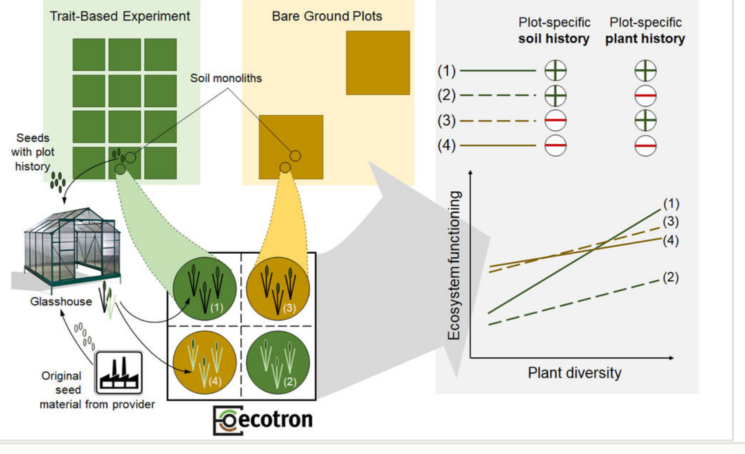

Figure 4. doi

Experimental design and hypotheses of the Ecotron Experiment. Briefly, four treatments will be established based on monoliths from a selection of the 9-year old Trait-Based Experiment (TBE; Ebeling et al. 2014) and from bare ground plots of the Jena Experiment as well as two seed sources: the respective plots and the original seed material that was used for the set-up of the TBE. (1) With plot-specific plant history and with plot-specific soil history; (2) without plot-specific plant history and with plot-specific soil history; (3) with plot-specific plant history and without plot-specific soil history; and (4) without plot-specific plant history and without plot-specific soil history. We expect the biodiversity–ecosystem function relationships to differ among the four treatments (see main text for details).

The Field Experiment – objectives and hypotheses

Studies on changes in biodiversity effects with community age (years since the start of the experiment) all have the problem that time (calendar year) is confounded with age. The Field Experiment (established in 2016 in preparation of this proposal; for design see Suppl. material 1; for one-page summary ["Cheat Sheet"], see Suppl. material 2) for the first time allows to compare communities of different ages at the same point in time. We set up the same communities in 2016 as we had set up in 2002 and can now observe them at ages 5 and 19 in 2020, 6 and 20 in 2021, and so on. To make the comparison, the communities of the same species compositions but different ages are located on the same plots. The '*with plant history, with soil history*' treatment is represented by the undisturbed soil and plant communities, which have been maintained since 2002 (Roscher et al. 2004). We also established a '*without plant history, without soil history*' treatment in order to replicate the soil situation as in 2002. Therefore, we used soil from a nearby agricultural crop field (no plant and no soil history from the old experiment; very similar to the conditions before the Jena Experiment was sown on a former agricultural field in 2002). In addition, we set up a treatment where the soil of the old experimental plot was broken up and mixed before sowing the new experiment with new seed material ('*without plant history, with soil history*'). The setup of this new experiment on the plots of the Main Experiment is a first significant step towards separating environmental correlates of time (such as climatic trends) from community age effects caused by plant–soil eco-evolutionary dynamics (Schnitzer et al. 2011, Eisenhauer et al. 2012a, Zuppinger-Dingley et al. 2014, Roscher et al. 2015, van Moorsel et al. 2018, Schmid et al. 2019). This allows us to experimentally explore community-age effects, such as eco-evolutionary soil history effects (plant community-specific soil history) and eco-evolutionary niche differentiation (plant community-specific plant history), on the strength of biodiversity effects independently of confounding temporal trends under the same climate conditions. In addition to the community-level analyses, we will employ a phytometer approach and plant species-specific assessments to study plant-specific eco-evolutionary responses to the experimental treatments in a standardized way and in concerted actions (Suppl. material 1).

According to the proposed mechanisms underlying strengthening BEF relationships in time (Eisenhauer et al. 2012a, Zuppinger-Dingley et al. 2014, Meyer et al. 2016), we expect the slope of the BEF relationship to differ among the treatments of the Field Experiment (Fig. 3): we hypothesize a steeper and more significant BEF relationship in the treatment '*with plant history, with soil history*' than in the treatment '*without plant history, with soil history*', because of increased niche differentiation in plants with eco-evolutionary history of coexistence. This means that low-diversity communities in the "*with plant history, with soil history*" treatment should perform worst in comparison to all other treatments, *e.g.*, due to the accumulation of plant antagonists and nutrient limitation (due to one-sided nutrient use); and the high-diversity communities in this treatment should perform best, *e.g.*, due to resource use complementarity and an accumulation of plant growth facilitators. The treatment '*without plant history, without soil history*' is predicted to have the shallowest BEF slope, because of lower niche differentiation in plant mixtures and missing plant community-specific soil effects (Fig. 3).

Preliminary results from the Field Experiment provide support for the prediction of a steeper slope in the '*with plant history, with soil history*' treatment for absolute and relative plant biomass production (Vogel et al. 2019). Moreover, soil nematode community composition and soil microbial functioning (carbon use efficiency) differed substantially among the experimental treatments (Vogel et al. 2019). Thus, already one year after establishment of the experiment, the BEF slopes of the treatments '*without plant history, without soil history*' and '*without plant history, with soil history*' differed significantly, suggesting that soil and plant history are both important, and motivating the complementary Ecotron Experiment (see below). This proposal for a new Research Unit will allow us to assess whether the effects consolidate and allows to probe the relevant mechanistic processes. Notably, the '*with plant history, with soil history*' treatment can only serve as a reference in the Field Experiment, because the respective plots were not disturbed like in the other treatments, and because the plant history treatment cannot be studied independent of the soil history treatment. Thus, plant history *versus* soil history effects can only be studied in the planned Ecotron Experiment.

Since the establishment of the Field Experiment has already been successfully accomplished in preparation of this proposal, there are no establishment risks, and the new research questions can be addressed immediately . The Field Experiment provides the ideal infrastructure for large collaborative initiatives on the mechanisms underlying BEF relationships (Fig. 2) and allows testing our overarching hypothesis as well as SP-specific hypotheses (see individual SP proposals).

The Ecotron Experiment – objectives and hypotheses

The comprehensive study of plant history and soil history effects requires complementary approaches, *e.g.*, for testing general relationships under field conditions (large species pool and random community mixtures in the Field Experiment), as well as more specific process and interaction assessments in highly-controlled setups (species- and interaction-specific effects and responses). The planned Ecotron Experiment allows us to do this along a well-established plant diversity gradient (for details on the design, see Suppl. material 4; for one-page summary ["Cheat Sheet"], see Suppl. material 5). It thus builds on the strengths of the Jena Experiment, while complementing the Field Experiment in several important aspects. While the Field Experiment and the Ecotron Experiment share the objectives provided above on the mechanisms of increasing BEF relationships over time, ***the unique objectives of the Ecotron Experiment are to (1) orthogonally separate plant history from soil history effects, (2) study plant species- and interaction-specific effects at all diversity levels, and (3) study the mechanisms underlying BEF relationships*** **via** ***sophisticated process measurements*** (see Table 1 for differences between the Field Experiment and the Ecotron Experiment). Thus, many SPs complement the assessments they also perform in the Field Experiment (mentioned above and in more detail in the SPs' proposals) with more detailed analyses of certain processes and interactions in the Ecotron Experiment.

We expect the steepest BEF slope in the treatment '*with plant history, with soil history*' (green, solid line in Fig. 4) due to increased plant complementarity at the high plant diversity (Fig. 1; van Moorsel et al. 2018) and specific plant-soil feedback effects (more detrimental ones at low plant diversity and more beneficial ones at high plant diversity; Eisenhauer et al. 2012a). In the treatment '*without plant history, with soil history*', we expect generally lower levels of ecosystem functioning, as plants may be less well protected against plant antagonists at low plant diversity and may have higher levels of niche overlap at high plant diversity (Fig. 1; green, dashed line in Fig. 4). In the treatment '*without plant history, without soil history*', we expect to find the shallowest BEF relationship (brown, solid line). While we hypothesize lower densities of plant-specific antagonists in the soil in this treatment (which is why EF might be higher than in the treatments with plot-specific soil history), plants at high plant diversity have not been selected towards elevated resource use complementarity (Fig. 1). Finally, we hypothesize slightly steeper BEF slopes in the treatment '*with plant history, without soil history*' (brown, dashed line), because the selection of plants towards increased defense (Fig. 1) may not be of benefit in a soil with low pathogen pressure (plant growth-defense trade-off). At high plant diversity, however, ecosystem functioning might be higher because of reduced niche overlap (Fig. 1).

Anticipated total duration of the project

Four years.

Research data and knowledge management

Regular meetings

The Central Coordination will organize at least ***two meetings per year*** (one in spring before the field season, one in autumn; '***Jena Retreat***') to guarantee a high level of transparency and information flow for all participating scientists and technicians. Typically, the Jena Retreat starts with a series of talks by each subproject (subproject-specific results and plans), which is followed by time for break-out groups for working on specific projects, planning of joint sampling campaigns, experiments, and analyses. These regular updates and opportunities to plan collaborations have been very successful in fostering interdisciplinary work in the Jena Experiment (as exemplified by the high number of joint publications in the consortium; >280 papers by April 2019, see Google Scholar account).

Communication, open platform, and workshops

In the present Research Unit, we propose cross-cutting projects, involving PIs and collaboration partners with different (complementary) expertise. All SPs will work and collaborate in the Field Experiment and Ecotron Experiment; an approach that has been proven successful in the past. Although the experiments are located in Jena and Bad Lauchstädt, respectively, the Research Unit is spread across Germany. Due to the size of the research group (currently >100 internal and external members), communication within the group is a major and important challenge. In addition to the Jena Retreats, we (mostly done by the scientific coordinator Dr. Anne Ebeling and the spokesperson Prof. Dr. Nico

Eisenhauer) permanently inform the Research Unit about latest news, upcoming projects, or plans *via* ***email*** and the ***webpage***. To foster multidisciplinary collaboration and avoid overlaps between research activities, the Jena Experiment has a ***coordinated system of project and paper proposals***, which are centrally registered (see data curator in Database section below). Following a common proposal template, information is presented to all members in a standardized way. All members of the Jena Experiment have the possibility to comment on the project proposal (which can also be submitted by external scientists) within a time frame of two weeks. Before submitting the respective manuscript to a scientific journal, it is again sent to all Jena Experiment members. To foster the education of our PhD students, we will organize ***statistics and writing workshops*** (one per year). Additionally, we will organize a yearly workshop for the ***female scientists***.

Database and international collaboration

From the past Research Units, we have learned that collaborative research requires a well-functioning database. ***The culture of data sharing and joint analyses is a great strength of the Jena Experiment and has already resulted in important contributions to the field*** (*e.g.*, Scherber et al. 2010, Allan et al. 2013, Meyer et al. 2016, Meyer et al. 2018). In addition, the Jena Experiment contributed data to impactful across-experiment syntheses (*e.g.*, Isbell et al. 2011, Isbell et al. 2015, Lefcheck et al. 2015, Craven et al. 2016, Guerrero-Ramírez et al. 2017, Craven et al. 2018) and has established the ***database infrastructure as well as data use and publication policies*** to facilitate similar work in the future. These measures have inspired other German research consortia (*e.g.*, the Biodiversity Exploratories, BEF China) that use very similar databases, data use and publication policies, as well as project and paper proposals (see below). Further, the Jena Experiment is regularly disseminating data to the scientific community. For instance, the Jena Experiment has ***published several thousand datasets at Pangaea*** and the ***iDiv Data Repository***.

The Jena Experiment has many collaborations in Germany and beyond, and researchers from the Jena Experiment have contributed to many syntheses and meta-analyses of BEF relationships in the last decade. Strong connections have been established to the other two long-term grassland biodiversity experiments in ***Cedar Creek*** (*e.g.*, Isbell et al. 2011, Reich et al. 2012, Thakur et al. 2015, Craven et al. 2018), and more recently to the global network of tree diversity experiments (***TreeDivNet***; Guerrero-Ramírez et al. 2017), ***BEF-China*** (Schuldt et al. 2019), and the ***Biodiversity Exploratories*** (M. Jochum et al., unpubl. data). The planned collaborations with the requested ***Mercator Fellows*** will further strengthen these international collaborations, *e.g.*, by closely linking to the other two running long-term grassland biodiversity experiments, ***BioCON*** and ***BioDIV*** (Reich et al. 2012).

In the proposed Research Unit, database infrastructure support will be provided by iDiv, including workshops on data management and open data, maintenance of database (helpdesk data upload; data upload and publication in iDiv Data Repository), archiving and back-up, hard- and software updates, structural adaptations for new experimental designs (*e.g.*, Ecotron), and transition of old and new databases. In addition, we request a ***data curator*** who will be responsible for data quality control and scientific computation help for PhD students, compliance with reproducible science principles (*e.g.*, R script publication), post-processing meta-data, update of Jena Experiment homepage, data policy implementation and checking, handling and registration of paper and project proposals, supervision of data transfer within and beyond the Research Unit, long-term time-series updates and publication, preparation of synthesis datasets, and data publication.

Other information

Local institutions provide unprecedented infrastructure support

In the requested Research Unit, the FSU Jena, iDiv, UFZ, and the MPI-BGC in Jena take over the full infrastructure costs (~EUR 1,590,000.00 for the requested four years), and all the requested funds are only related to scientific projects. This is an exceptional investment into the requested Research Unit and reflects the major interest of the collaborating institutions in this initiative.

Potential impact on the research area and local research environment

The Jena Experiment is one of the longest-running biodiversity experiments in the world, and recent research has shown that these few long-term experiments (Jena, BioCON and BioDIV) are particularly valuable for studying BEF relationships and the underlying mechanisms, including the relevance of community assembly processes (*e.g.*, Reich et al. 2012, Guerrero-Ramírez et al. 2017) and eco-evolutionary dynamics (*e.g.*, Zuppinger-Dingley et al. 2014, van Moorsel et al. 2018). The Jena Experiment with its integrative and multidisciplinary approach thus is ideally positioned to advance BEF research and inform relevant decision bodies about the consequences and mechanisms of biodiversity change. This research is not only based on the unique long-term plots of the Jena Experiment, but also on the setup additional field treatments focusing on soil history effects as well as on the local research infrastructure of the iDiv Ecotron. This facility was recently established to study the role of biotic interactions across trophic levels and above-belowground compartments to zoom in on the mechanisms of BEF relationships in complex communities (Eisenhauer and Türke 2018). The novel and complementary technologies applied in the BEF context for the first time (see above) will guide the field into a more process- and mechanism- centered direction. Taken together, we believe that the proposed research consortium in combination with the well-established Field Experiment and Ecotron facility will enable unique advancements of this area of research and produce the respective inspiring research outputs.

In addition to this international scientific impact, the proposed Research Unit bundles expertise in Central Germany and beyond, and links unique experimental infrastructures (Jena Experiment and iDiv Ecotron) in an innovative way. Moreover, as outlined above, Jena Experiment researchers have started collaborations with other large German research consortia, such as synthesis work with BEF China (Schuldt et al. 2019) and the Biodiversity Exploratories. This will not only facilitate collaboration among Jena Experiment

PIs, but also secure funding and scientific support for the continuation of the long-term plots of the Jena Experiment that have served as a platform for national and international collaboration. Thus, the proposed Research Unit will significantly increase the international visibility and recognition of the Jena Experiment, the Ecotron, and the PIs involved in this project, and, as a consequence, strengthen Germany's role in functional biodiversity research.

Measures to advance research careers

An important means to support the development of early career researchers is the ***frequent scientific exchange*** between PhD students, postdocs, and PIs, which is greatly facilitated by two scientific and organizational meetings per year. PhD students present their research plans and results twice a year, which is an ideal practice and allows learning of the ***skills for presenting their research and discussing their ideas*** at international conferences. Further, early career researchers have the possibility to attend ***workshops on statistical analyses and paper writing*** organized by the Central Coordination of the Jena Experiment. Those workshops have always been very helpful for PhD students and thus are very well attended. The last paper writing workshop was organized by the PhD students themselves to let them define the input they needed from speakers and supervisors. Moreover, the PhD students have meetings at every Jena Retreat and are represented by ***two elected PhD representatives***. The contents of the PhD meetings are discussed in the whole plenum. Finally, early career researchers greatly benefit from the ***integrative and multidisciplinary approach***, such as exemplified by the many successful scientific careers of Jena Experiment alumni.

In addition to these options provided by the Jena Experiment itself, PhD students will have the possibility to attend courses at the ***Graduate School of iDiv***, called yDiv. While it will not be obligatory for PhD students to participate in a graduate school, many students will be hosted in Jena and Leipzig, and/or will have many scientific meetings and experimental samplings in that region, which is why they will have the opportunity to combine their stays in Central Germany with yDiv courses. yDiv offers young researchers unmatched opportunities of tutoring, teaching, and networking. The uniqueness of the curriculum stems from active exchange between theoreticians and empiricists in ecology. In addition to ***research-centered classes, yDiv offers different soft skill courses***, such as presentation skills, scientific writing, proposal writing, 'how to manage your supervisor', good scientific practice, supervision of students, career consultation, and many more.

National and international cooperation and networking

As outlined above, the Jena Experiment has always been an ***open research platform*** for national and international collaboration, such as in the framework of the former EU-network EXPEER (Distributed Infrastructure for EXPErimentation on Ecosystem Research). ***Any researcher can submit project proposals to the scientific coordination of the Jena Experiment***. After an initial check of potential overlaps with already planned work and potential support with refining the proposal, project proposals are sent to all Jena Experiment members to stimulate scientific discussion and collaboration and to guarantee full transparency. Many researchers have acquired additional/their own third-party funding to conduct their research in the Jena Experiment, such as DBU-scholarships for PhD students (German Federal Environmental Foundation), PhD scholarship by the Heinrich Böll Foundation, a DFG-funded Emmy Noether group to Nico Eisenhauer, and an NSF-funded project led by Dr. Andrew Kulmatiski that experimentally combined the long-term biodiversity experiments in Cedar Creek and Jena. These projects exemplify the Jena Experiment serving as an experimental platform for international researchers (even attracting funds by non-German research foundations) and the strong interest of scientists to conduct their research in the Jena Experiment.

The Jena Experiment has organized many ***international conferences and workshops***, facilitating scientific exchange and collaboration among different experiments. Data from the Jena Experiment frequently enters international ***syntheses and meta-analyses***. In addition, first syntheses have been conducted and are in preparation integrating data from the Jena Experiment and BEF China (Schuldt et al. 2019) and the Biodiversity Exploratories, respectively. Continued exchange is guaranteed through Nico Eisenhauer's involvement as a PI in the new International Research Training Group TreeDì in the framework of BEF China, as well as the lead roles of Markus Fischer and Wolfgang Weisser in the Biodiversity Exploratories, and of Stefan Scheu in EFForTS. Moreover, as head of the MyDiv experiment (Ferlian et al. 2018), Nico Eisenhauer is member of TreeDiv Net, an ***international network*** of tree diversity experiments. First joint data analyses of grassland and forest biodiversity experiments suggest that integration is possible and may allow identifying general BEF patterns and mechanisms across ecosystem types (Guerrero-Ramírez et al. 2017, Schuldt et al. 2019).

Requested budget for coordination of the Research Unit

Description of how joint objectives and the joint work programme will be implemented in the coordination project

As outlined above, the described scientific objectives will be achieved *via* a ***plethora of communication and interaction channels*** that have proven successful in facilitating integrative BEF research. Regular meetings (***Jena Retreats***) provide the basis for mutual trust and collaboration. We will use multiple communication channels to guarantee the highest level of transparency, including regular ***email updates***, ***webpage***, ***Twitter***, and ***Google Scholar*** accounts, a ***common database***, a clear ***data use policy***, and a common ***project- and paper proposal system***. These means as well as central coordination of experimental setups and sampling campaigns will be strongly supported by SP Z1 (see SP Z1 proposal). Accordingly, the spokesperson has made sure that all research plans proposed in this Research Unit are highly complementary and all contribute to the common goal to study biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships.

Requested modules

Coordination module

As outlined above, there are multiple needs of the Research Unit that require a central and flexible budget. For instance, in the past funds from the Coordination Module were used to cover ***unforeseen repair or replacement of infrastructure and central equipment***, additional ***workshops and analyses in exceptional circumstances***, such as extreme climate events (*e.g.*, Wright et al. 2015), and ***additional management and measurement campaigns***, including repeated or additional measurements. A total of EUR 40,000.00 coordination funds are requested (standard rate of EUR 10,000.00 per year).

Total sum of requested funds in 'Coordination Module': EUR 40,000.00

Network Funds Module *(Funding for Staff, Direct Project Costs and Instrumentation)*

Notably, substantial financial support by the contributing institutions, particularly of the FSU Jena (funding the Scientific Coordinator, a technician, and gardeners) facilitates the scientific network. In addition to the database infrastructure support provided by iDiv, we request a **data curator (50% E13)**, who will be responsible for data quality control and scientific computation help for PhD students, compliance with reproducible science principles, post-processing meta-data, Jena Experiment homepage, data policy implementation and checking, supervision of data transfer within and beyond the Research Unit, long-term time-series updates and publication, and preparation of synthesis datasets.

Gender Equality Measures in Research Networks Module

Similar to the previous phases of the Jena Experiment, the proportion of female PIs is relatively high (~35%), surpassing the proportion of female professors at German universities by far (~20% in 2015). ***Female researchers are involved in all proposed SPs***, either as PIs or as key contributors, which shows that female researchers are well integrated into the network and also hold leading positions, *e.g.*, as PIs in the Central Coordination (SPZ). Notably, the careers of several female researchers have benefited from the Jena Experiment as a Research Unit in the past. They now hold professorships or permanent positions at various universities or research institutes. In the last Research Unit, the proportion of female researchers was ~42% among postdocs and ~69% among PhD candidates. Obtaining a PhD is a critical phase in a scientific career towards a professorship as females often wish to start a family. If they do not receive any help to balance their time-consuming academic work when having their first child, and in addition receive support to explore future career options, they often drop out of science. With the proposed large group of young female scientists and more experienced PIs – with kids – there is great potential for ***role model interactions*** that will show that it is possible to combine career and family, also as a female scientist. In the proposed Research Unit, we explicitly aim to engage specific tools to support young female researchers to build up a successful academic career.

During the past 17 years, we have gained experience with ***three important means to support female researchers*** (requested funds: EUR 60,000.00; Coordination; EUR 15,000.00 per year). First, we organized yearly ***scientific workshops*** only for the female researchers of the Research Unit. The female scientists attending rated those workshops as very important as they were organized particularly to meet their needs (*e.g.*, time for data analysis and writing and discussions in female-only groups, professional training in specific statistical analyses with female trainers and experts, and organized child care during the workshop). The workshops have been extremely successful with several publications being initiated and written up and new projects developed with females as leading PIs. For these reasons, we plan to continue with those yearly workshops in the period as specified in the current proposal. The second important means is ***flexible support***. The career-limiting issues that female researchers may experience due to pregnancy, maternity leave, and childcare duties, are very individual. These can only be addressed by having a flexible support system. For instance, some female researchers needed some family-friendly support, such as child-care during workshops, conferences, or school holidays. We will further support female researchers during pregnancy and maternity leave by, *e.g.*, equipping home offices or giving field assistance by student helpers. We would like to keep this flexibility to provide individual support. Third, another measure that has been proven successful to empower females striving for a career in science, is the provision of ***mentoring programs*** to promote leadership qualities, improve work-life balance, or to support applications and interviews for professorships. We will set up mentoring groups, where peers support each other in an organized manner. Each year, female scientists in the group will be asked to specify which type of course or activity would be the most appropriate. Moreover, the more advanced female PIs will be asked to give role model talks, *e.g.*, during lunch at Jena Retreats.

Total sum of requested funds in 'Gender Equality Measures': EUR 60,000.00

Project-Specific Workshop Module

We are planning to organize at least one synthesis workshop that brings together data from multiple experiments across ecosystems to study long-term BEF relationships and their context-dependency and to foster international collaboration and networking. This workshop will facilitate the synthesis work of the requested plant postdoc in SPZ (WP6) and will help consolidating the Jena Experiment as a global leader in BEF synthesis. We are not requesting any money in this proposal, but will apply to sDiv workshop funds or use coordination funds (Coordination Module).

Mercator Fellow Module

To foster scientific exchange with international colleagues and add complementary expertise to the consortium, we plan to invite four Mercator fellows with expertise in belowground ***plant-plant- and plant-fungal interactions*** (Dr. Liesje Mommer), ***soil biogeochemistry and element cycling*** (Dr. Kevin Mueller), ***data synthesis*** and strong link to long-term biodiversity experiments in Cedar Creek (Dr. Forest Isbell), and ***plant physiology and plant eco-evolutionary dynamics*** (Dr. Jeannine Cavender-Bares). For each of these international collaborators, we calculated with a four-week stay in Jena or Leipzig that can also be split into multiple visits. For each Mercator Fellow, we calculated with the monthly DFG standard salary for professors (EUR 8,675.00) and travel costs of EUR 2,500.00 per fellow. However, we are requesting money for only two of the four Mercator Fellows in this proposal and will apply to sDiv sabbatical funds and/or use coordination funds (Coordination Module).

Total sum of requested funds in 'Mercator Fellow Module': EUR 22,350.00

Public Relations Module

The efficient communication of scientific findings to the public and policy makers is essential for the broad appreciation of the consequences of biodiversity change. During the last years, there has been increasing interest in the research of the Jena Experiment by the public (*e.g.*, at the yearly ***Open Day***; requested funds: EUR 5,000.00) as well as print, radio, and TV press, also facilitated by the outstanding work of iDiv's press office (>100 media coverages; reaching >15 million people between November 2014 and April 2019). During the running funding period, we regularly offered information for ***press releases and institutional newsletters***. An exceptionally successful tool to communicate the rationale and results of the Jena Experiment is the new ***image movie*** that is available in English and German. Moreover, the Jena Experiment now has its own ***Twitter***, and ***Google Scholar*** accounts. In the requested Research Unit, we plan to represent the Jena Experiment at important ***local public relations events***, such as the MINT exhibition in Jena and the Long Night of Sciences in Leipzig. The Jena Experiment also serves as a ***teaching platform***. We gave regular excursions for groups from the University of Bayreuth (course "Monitoring and Experiments in Ecology"), FSU Jena ("Ecological Excursion", "Field Practical"), University of Koblenz, University of Bonn (module "Biodiversity and Ecosystem Functions"), the graduate school of iDiv (yDiv), the summer school of iDiv, and the graduate school of the MPIs (summer school IMPRS). We propose to follow up this active role in public relations and teaching in the proposed Research Unit and feel encouraged that the relevance of the results of the Jena Experiment is widely appreciated, such as exemplified by the recent speech at the iDiv Ecotron inauguration by Karl Eugen Huthmacher, Department Head at the German Federal Ministry of Education and Research (BMBF), who stated that "…biodiversity change is at least as important as climate change for humans". Moreover, a new, up-to-date homepage is needed that will be developed with support from the FSU Jena.

Total sum of requested funds in 'Public Relations Module': EUR 5,000.00

Project requirements

Employment status information

Eisenhauer, Nico; Prof. Dr.; W3 Professor at Leipzig University, currently DFG-funded through iDiv; permanent position at Leipzig University.

First-time proposal data

N.A.

Composition of the project group

The Coordination of the proposed Research Unit will be supported by the Scientific Coordinator Dr. Anne Ebeling (FSU Jena, permanent), the gardener team and field technician of the Jena Experiment (all FSU Jena, permanent), a foreign language secretary (Kathrin Greyer; iDiv, fixed-term contract), the Ecotron Scientific Coordinator Dr. Anja Schmidt (iDiv, fixed-term contract), and the two Ecotron technicians (one iDiv-funded, fixed-term contract; one UFZ-funded, permanent contract).

Cooperation with other researchers

See above for collaborations with other large research consortia. Moreover, Prof. Dr. Bernhard Schmid played an important role in the design of the Field Experiment, and despite his recent retirement, he will stay involved as an essential collaborator and advisor. Moreover, Prof. Dr. Birgitta König-Ries was a PI in the former database project of the Jena Experiment and is a leading expert in data management for ecological research, FAIR data, and reproducible research; she will provide advice regarding data management and publication.

Scientific equipment

Coordinating the Research Unit also means to provide all scientist with reliable data on plot-specific soil properties and site specific meteorological data. Therefore, a main ***meteorological station*** as well as a ***CanBus system*** were installed in 2002, and in the past, these data have been shown to be of central relevance for long-term times-series analyses within and syntheses beyond the Jena Experiment. After 17 years of operation, the technical equipment has to renewed and needs regular maintenance. The maintenance itself will be done by a technician from the central project.

Weather Station Maintenance (EUR 2,500.00 per year): EUR 10,000.00

CanBus System Renewal: EUR 9,110.33

CanBus Maintenance (EUR 2,400.00 per year): EUR 9,600.00

Total sum of requested funds in ‘Scientific equipment’: EUR 28,710.33

Overall budget and requested personnel

Total sum of requested funds in the Coordination Proposal: 300.060,00 €

Total sum of requested funds in the Research Unit: 5,317,500 €

Requested number of PhD positions: 11 (65%)

Requested number of postdocs: 1 (100%)

Requested number of data curators: 1 (50%)

Requested number of technicians: 4

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Funding program

Research Unit (Forschungsgruppe)

Conflicts of interest

The authors have declared that no competing interests exist.

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Supplementary materials

Suppl. material 1: Design of the Field Experiment doi

Authors: Eisenhauer et al.
Data type: Text
Brief description: Detailed design of the Field Experiment
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Suppl. material 2: Cheat sheet Field Experiment doi

Authors: Eisenhauer et al.
Data type: Text
Brief description: Brief description of the Field Experiment
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Suppl. material 3: Plant species list doi

Authors: Eisenhauer et al.
Data type: Table
Brief description: Plant species lists of the Field Experiment and the Ecotron Experiment
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Suppl. material 4: Design of the Ecotron Experiment doi

Authors: Eisenhauer et al.
Data type: Text
Brief description: Detailed design of the Ecotron Experiment
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Suppl. material 5: Cheat sheet Ecotron Experiment doi

Authors: Eisenhauer et al.
Data type: Text
Brief description: Brief description of the Ecotron Experiment
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Appendix I: Design of the Field Experiment

The **Field Experiment** involves a total of 240 subplots: 80 plots (size 1.5 x 3 m) of the Main Experiment (Roscher et al. 2004) with the three treatments described above (**Fig. 3**; see also **Fig. A1a**). The location in the plot is randomized. In addition, we set up monocultures from all species in the Jena Experiment species pool (60 species) on plots of 1 x 1 m, using the same soil preparation as in the treatment *'without plant history, without soil history'*; monoculture plots *'with plant history, with soil history'* are still available from the old set up in 2002. This resulted in two sets of monocultures (120 monocultures in total). We were not able to set up monocultures *'without plant history, with soil history'*, because the old monocultures were too small to further subdivide them into subplots. This limitation is being addressed by the complementary Ecotron Experiment.

For the *'without plant history, with soil history'* treatment in the Field Experiment, the upper 5 cm of soil were removed, and the underlying soil was homogenized and freed of large roots down to a depth of 30 cm (**Fig. A1**). Belowground plastic barriers (1.5 m long, 0-30 cm soil depth) were installed to avoid fast lateral colonization by soil organisms (**Fig. A1b**). For the *'without plant history, without soil history'* treatment, the upper 30 cm of the soil profile was exchanged by soil from an adjacent agricultural field site with similar conditions to those during the establishment of the Main Experiment in 2002 (~150 m^3 of soil in total). Both treatments were then sown with the plant communities according to the initial design of the Main Experiment (1000 germinable seeds/m^2; **Fig. A1c**; Roscher et al. 2004). Seed material was derived from a commercial seed supplier and therefore had no site-specific plant history. This experimental setup allows us to identify effects caused by soil biota (plant antagonists and plant growth facilitators). Soil nutrients and seed banks were not manipulated, but are measured to account for potential differences when comparing data for the 1- or 2-year-old new communities (2017, 2018, and so on) with data collected in years 2003, 2004, and so on for the now old communities.

All subprojects will perform their field sampling campaigns in concerted actions, such as shortly before the early summer harvest at peak plant biomass. Soil and plant samples will be shared to facilitate synthesis of the different assessments. In addition to plant community-level studies, we will employ a **phytometer approach** (e.g., Scherber et al. 2006, Eisenhauer et al. 2009, Lipowsky et al. 2011) to study plant species-specific eco-evolutionary responses to the experimental treatments in a standardized way (led by SP10). For this purpose, we selected a pool of eight plant species representing different functional groups (grasses, legumes, small herbs, and tall herbs) with two species per functional group (**Appendix III**). Specifically, this includes *Plantago lanceolata* and *Plantago media* as representatives of small herbs, *Geranium pratense* and *Ranunculus acris* as representatives of tall herbs, *Alopecurus pratensis* and *Trisetum flavescens* as representatives of grasses, and *Lotus corniculatus* and *Medicago x varia* as legumes. Phytometer species selected for the Field Experiment overlap in part with the Ecotron Experiment (**Appendix III**). In the Main Experiment (Roscher et al. 2004), which is the basis for the Field Experiment, these species occur on different numbers of plots (11-18 plots). Due to space limitations and because we do not want to disrupt plant communities in the target plot, we will grow not more than two of the selected phytometer species on a single plot that are part of the established target plots community. We tried to have each of the phytometer species in ten plots along the diversity gradient. Some species will have only eight or nine replicates though. Phytometers will be grown as offspring from seed families collected in the treatment *'with plant history, with soil history'*. We will grow phytometers from four seed families per source plot and will use three offspring per seed family to be planted in a target plot. The full design gives 75 plot-species-combinations x 4 seed families x 3 offspring x 3 treatments = 2,700 plants). The design is flexible in various possibilities to reduce the number of studied plants for certain subproject-specific measurements. In addition to the study of 'selected' plants in the full design of the Field Experiment, transplant plants grown from the origin seed material (i.e., plants without selection history) will be grown in subplots *'with plant history and with soil history'*; i.e., among selected plants in their otherwise undisturbed communities. Therefore, mother plants have already been growing in the greenhouse in preparation of this proposal; the plants are growing well, and offspring will be transplanted to the Field Experiment.

In addition to the phytometer approach, **plant species-specific assessments** will be performed in collaborative studies using resident plant individuals. Twelve plant species were selected (three per plant functional group) that are sufficiently replicated in plots with low (1 and 2 species) and high plant diversity (8 and 16 species) and can thus be studied at the species-level in the treatment *'with plant history, with soil history'*. SP8 will measure plant defense traits on all twelve resident plant species, and SP11 will determine the genetic diversity. On three selected plants out of this pool (*Plantago lanceolata*, *Medicago x varia*, and *Trisetum flavescens*), SP7 will perform an herbivory experiment. Three individuals per plant species and plot will be infested with the generalist herbivore *Spodoptera littoralis* and three other plant individuals will serve as 'control plants' (without herbivory). On those six resident plant individuals per plot, SP7 will measure volatiles, and SP8 will intraspecific variability in shoot and root traits. Moreover, SP5 will measure community-level arthropod communities, predation and herbivory, and the response (arthropod communities, herbivory, and predation) to the intra-specific variability measured by the other SPs on all twelve resident plant species.

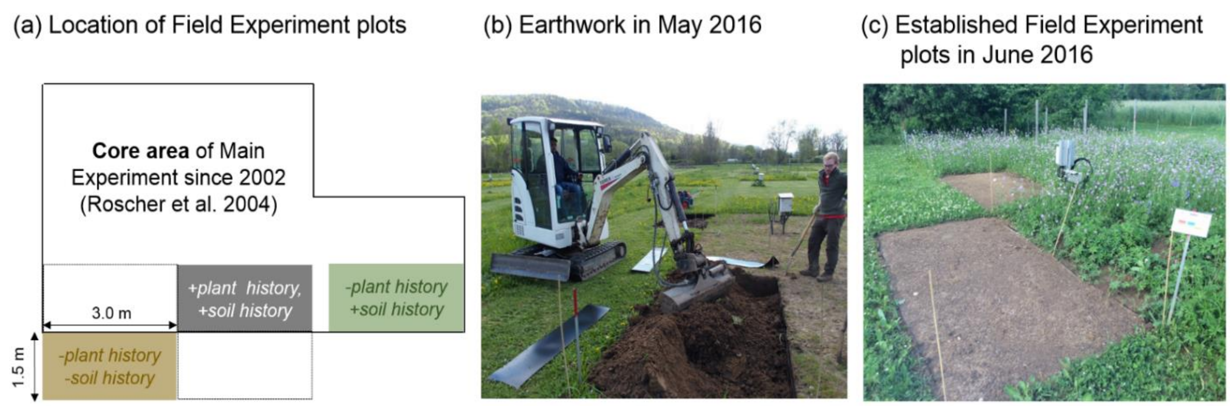

Figure A1. (a) *Spatial arrangement of the subplots of the Field Experiment in the plots of the Main Experiment (Roscher et al. 2004). The Field Experiment comprises three treatments: 'with plant history, with soil history', 'without plant history, with soil history', and 'without plant history, without soil history'. Locations of treatments per plot were randomized.* ***(b)*** *Photograph showing the earthwork and installation of belowground plastic barriers in May 2016.* ***(c)*** *Finalized plots shortly after sowing.*

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Appendix V

Table A3. *List of plant species used in the framework of the requested Research Unit. The Field Experiment allows us to employ (1) plant community-level approaches, covering all 60 plant species sown in the Field Experiment, and (2) plant species-specific assessments (selected plant species resident in the plots of the Field Experiment). In addition, we will use eight species of our species pool for phytometer approaches, and two for additional mesocosm experiments.*

	Field Experiment	Residents	Phytometers	Ecotron Experiment	Mesocosm experiments
Grasses					
Alopecurus pratensis	x	x	x		
Anthoxanthum odoratum	x			x	
Arrhenatherum elatius	x				
Avenula pubescens	x				
Bromus erectus	x				
Bromus hordeaceus	x				
Cynosurus cristatus	x				
Dactylis glomerata	x			x	
Festuca pratensis	x				
Festuca rubra	x	x			
Holcus lanatus	x			x	
Luzula campestris	x				
Phleum pratense	x				
Poa pratensis	x				
Poa trivialis	x				
Trisetum flavescens	x	x	x		
Legumes					
Lathyrus pratensis	x	x			
Lotus corniculatus	x	x	x		
Medicago lupulina	x				
Medicago x varia	x	x	x		
Onobrychis viciifolia	x				
Trifolium campestre	x				
Trifolium dubium	x				
Trifolium fragiferum	x				
Trifolium hybridum	x				
Trifolium pratense	x				
Trifolium repens	x				
Vicia cracca	x				

	Field Experiment	Residents	Phytometers	Ecotron Experiment	Mesocosm experiments
Small herbs					
Ajuga reptans	x				
Bellis perennis	x				
Glechoma hederacea	x				
Leontodon autumnalis	x				
Leontodon hispidus	x				
Plantago lanceolata	x	x	x	x	x
Plantago media	x		x		
Primula veris	x				
Prunella vulgaris	x				
Ranunculus repens	x	x			
Taraxacum officinale	x				x
Veronica chamaedrys	x	x			
Tall herbs					
Achillea millefolium	x				
Anthriscus sylvestris	x				
Campanula patula	x				
Cardamine pratensis	x				
Carum carvi	x				
Centaurea jacea	x				
Cirsium oleraceum	x				
Crepis biennis	x	x			
Daucus carota	x				
Galium mollugo	x				
Geranium pratense	x	x	x		
Heracleum sphondylium	x				
Knautia arvensis	x				
Leucanthemum vulgare	x			x	
Pastinaca sativa	x				
Pimpinella major	x				
Ranunculus acris	x	x	x	x	
Rumex acetosa	x				
Sanguisorba officinalis	x				
Tragopogon pratensis	x				

Appendix IV: Design of the Ecotron Experiment

The iDiv Ecotron is a joint research platform from iDiv and the Helmholtz Centre for Environmental Research – UFZ (Eisenhauer & Türke 2018). It is an indoor research facility housing a set of 24 identical experimental units, called EcoUnits, each of which can harbor one to four isolated ecosystems confined in compartments (**Fig. A2**). Species assemblages within ecosystems can be manipulated above and below the ground, varying horizontal diversity (i.e. the number of species within a trophic level) and vertical diversity (i.e. the number of trophic levels). Ecological processes can be measured with non-invasive methods, while environmental conditions within EcoUnits are either controlled for the whole set of replicates (air temperature) or for each replicate individually (e.g., irrigation, illumination, soil temperature; **Fig. A2**). The Ecotron allows for the construction of complex ecosystems resembling near-natural conditions but with the possibility to eliminate or reduce the variance from unknown factors (e.g., by controlling environmental conditions) and to easily measure most of the variables influencing ecological processes and, thus, the mechanisms underlying BEF.

Twenty-three plots of species pool 2 of the Trait-Based Experiment (TBE) in the Jena Experiment (established in 2010; Ebeling et al. 2014) were selected to cover a plant diversity gradient of 1, 2, 3, and 6 species (6 plant species mixtures serve as a higher-diversity reference). Six plant species of species pool 2 were selected due to the overlap of plant species with the Field Experiment, the equal (three species each) representation of grasses (*Anthoxanthum odoratum, Holcus lanatus, Dactylis glomerata*) and herbs (*Plantago lanceolata, Leucanthemum vulgare, Ranunculus acris*), and the dissimilarity in temporal resource acquisition traits (Ebeling et al. 2014), which may increase over time (**Fig. 1**). In spring 2021, we will excavate two monoliths of each of the 22 selected TBE plots, and additional four monoliths of the selected 6-species plot (48 monoliths in total; **Fig. 4, Table A4**). The monoliths will have a depth of 0.8 m and a diameter of 0.5 m. Those monoliths will represent Ecotron treatments with soil history (**Fig. 4**). In addition, we will excavate 48 monoliths from the bare ground plots of the Jena Experiment. These plots have been maintained without vegetation cover since 2002 and will represent treatments without soil history (**Fig. 4**). These monoliths are ideal for this purpose as they have the same soil characteristics as the experimental plots (pH, sand content etc.). One EcoUnit will harbor four monoliths (**Fig. A2c**; note that aboveground glass walls will separate the four monoliths, such as installed in **Fig. A2b**), two with plot-specific soil history (from the same TBE plot) and two without soil history (from the bare ground plots; **Fig. 4**).

The vegetation will be gently removed from the monoliths with plot-specific soil history, such as already successfully done in the Field Experiment, to start with equal conditions across soil history treatments. The two soil history treatments will be crossed with two plant history treatments by transplanting pre-grown seedlings of the respective plant community composition of the TBE at equal densities at a distance of ~5 cm among plant individuals (~360 plant individuals m^{-2}; ~70 per monolith). One treatment will be planted with pre-grown plants from seeds collected in the respective TBE plot in 2019 (with plot-specific plant history). As a reference, the same plant species will be grown from seed material that was used in 2010 (**Fig. 4**), when the TBE was set up. These plants will not have a plot-specific plant history. Plants will be pre-grown in plot-/treatment-specific soil that will also be used for the **Ecotron Experiment**. This means that in each EcoUnit, we will establish four treatments with the same plant species composition and plant density: (1) *'with plant history, with soil history'*; (2) *'without plant history, with soil history'*; (3) *'with* *plant history, without soil history'*; and (4) *'without plant history, without soil history*' (**Fig. 4**). The experiment will run for ~6 months before it gets destructively sampled.

Table A4. A. *Table providing an overview of the different treatments in the planned Ecotron Experiment, covering a gradient on plant species richness and functional diversity in temporal resource use (Ebeling et al. 2014) crossed with two treatments of plant history and soil history, respectively. The number of replicates per plant species richness level is given in brackets.* ***B.*** *Representation of the different plant species (for full names see text) in the different plant species richness levels. Given is the number of occurrences in different plant communities. Each plant species can be investigated along the plant species richness gradient.*

A. Treatments	**Levels**			
Plant species richness	1 (6 reps)	2 (9 reps)	3 (7 reps)	6 (2 reps)
FD plant temporal resource use	1	1-4	2-4	4
Plant history	with history	without history		
Soil history	with history	without history		
B. Plant species	**monocultures**	**2-species mix**	**3-species mix**	**6-species mix**
Ant odo (12)	1	4	5	2
Dac glo (12)	1	4	5	2
Hol lan (9)	1	3	3	2
Leu vul (7)	1	2	2	2
Pla lan (10)	1	3	4	2
Ran acr (7)	1	2	2	2

We will establish a **phytometer experiment** in the Ecotron Experiment using genotypes of the model species *Plantago lanceolata* (led by SP10). Three mother individuals will be collected each at low (monoculture) and high (8-species mixture) diversity with 8 years selection history in the TBE. The mother individuals will be vegetatively propagated and one offspring of each genotype will be transplanted into those units of the Ecotron Experiment, which contain *P. lanceolata* in the original composition (= 10 communities x 4 treatments x 6 individuals = 240 plants). This experiment will test if genetically identical plants show adaptive phenotypic plasticity and epigenetic variation in response to the actual environment (local plant diversity, plant community and soil history) and if these responses depend on the selection history of the genotypes.

Similar to the herbivory experiment in the Field Experiment, the generalist herbivore *Spodoptera littoralis* will be used by SP5 to induce herbivory on three *Plantago lanceolata* individuals per treatment, and three individuals will serve as 'control' plants. This will be only realized in treatments that have *Plantago lanceolata* in the species pool, summing up to a total of 240 plant individuals (10 plots x 4 soil/plant history treatments x 2 herbivory treatments á 3 individuals). Shortly before the harvest of the experiment, the focal plant individuals will be screened for volatiles (SP7), metabolites and shoot traits (SP8).

In concerted campaigns, SP1 will study species-specific mycorrhization rates and mycorrhizal diversity as well as mycorrhizal and fungal diversity at the community level; SP2 will investigate species-specific protist communities; SP3 will sequence the microbiome of the *Plantago* phytometers and the root microbiome of a subset of the other plant species; SP7 will study constitutive (repeated measurements) and herbivore-induced VOC emission; SP8 will perform metabolomics analyses on leaf and root tissue, phloem and root exudates of *Plantago* phytometers, and will study species-specific traits of all plant species; SP9 will study community-level DOM and DOC (repeated measurements); SP4 will study plant species-specific phenology, soil invertebrate feeding activity and community composition and traits, root growth and turnover, and soil microbial biomass (all repeated measurements); SP5 will examine herbivore effects on plant performance in a common *Plantago* experiment (where SP7 and SP8 will study the plant's volatile emissions, metabolome, and defense traits, respectively); SP6 will study soil food webs to infer belowground herbivory and the dominance of different soil energy channels; SP10 will lead the *Plantago* phytometer study; and SPZ will study plant species-specific shoot biomass, community-level root biomass, soil and plant community-level C, N, and P concentrations, and will coordinate the field component of the study (e.g., selection of plots and sampling locations, collection of seeds, excavation of soil cores).

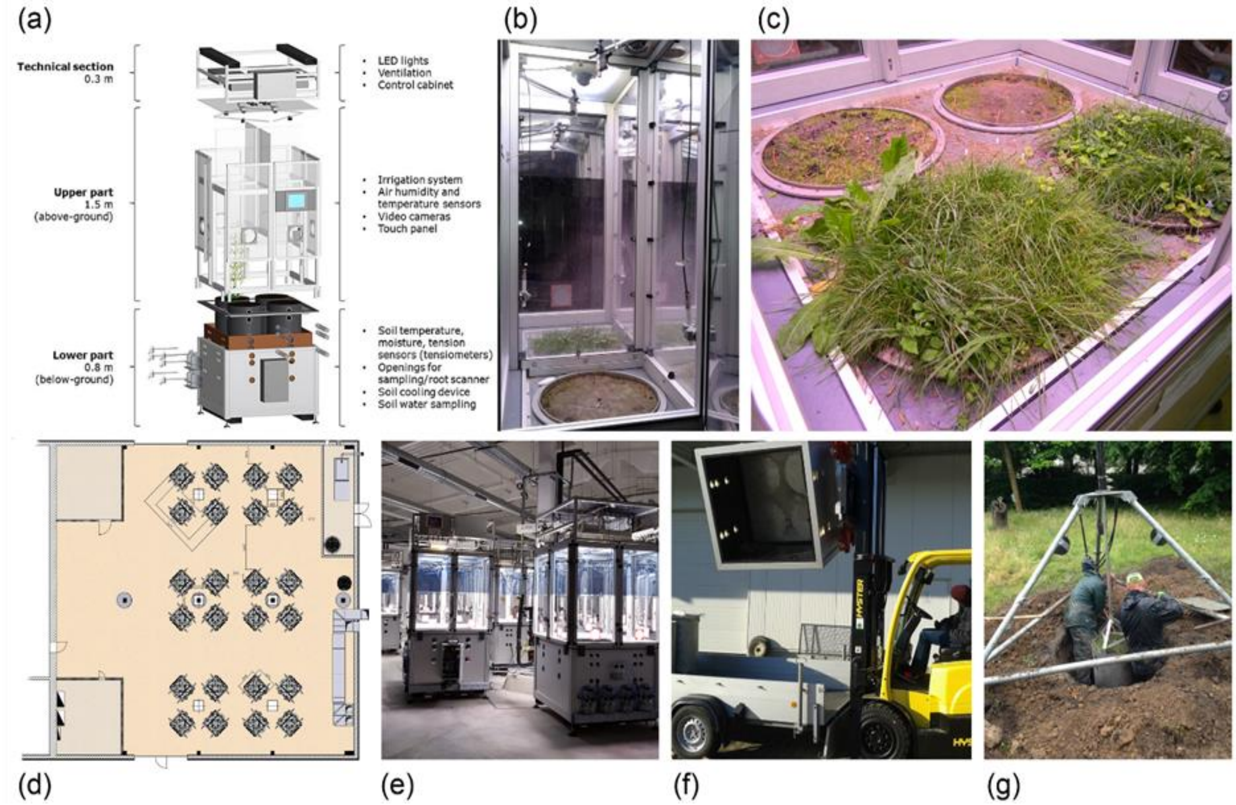

Figure A2. *Experimental infrastructure in the iDiv Ecotron in Bad Lauchstädt, Germany.* ***(a)*** *Schematic depiction of one experimental unit ("EcoUnit") with technical equipment.* ***(b)*** *Photograph showing the automated irrigation system, camera system, sensors, and inner walls of one half of an EcoUnit.* ***(c)*** *Photograph of four lysimeters in one EcoUnit without inner walls. Lysimeters can be manually filled with new soil and plants (the two lysimeters in the back where germination just started) or intact monoliths can be excavated in the field and incubated in the Ecotron (the two lysimeters in the front with the dense vegetation).* ***(d)*** *Schematic depiction of the spatial arrangement of the 24 EcoUnits of the iDiv Ecotron (from above) in the climate-controlled Ecotron hall.* ***(e)*** *Photograph of some of the EcoUnits in the Ecotron hall.* ***(f)*** *Photograph showing one exemplary lower part of an EcoUnit that is transported and turned with the help of a forklift.* ***(g)*** *Photograph of the excavation of a soil monolith in the Botanical Garden in Leipzig in preparation of this proposal.*

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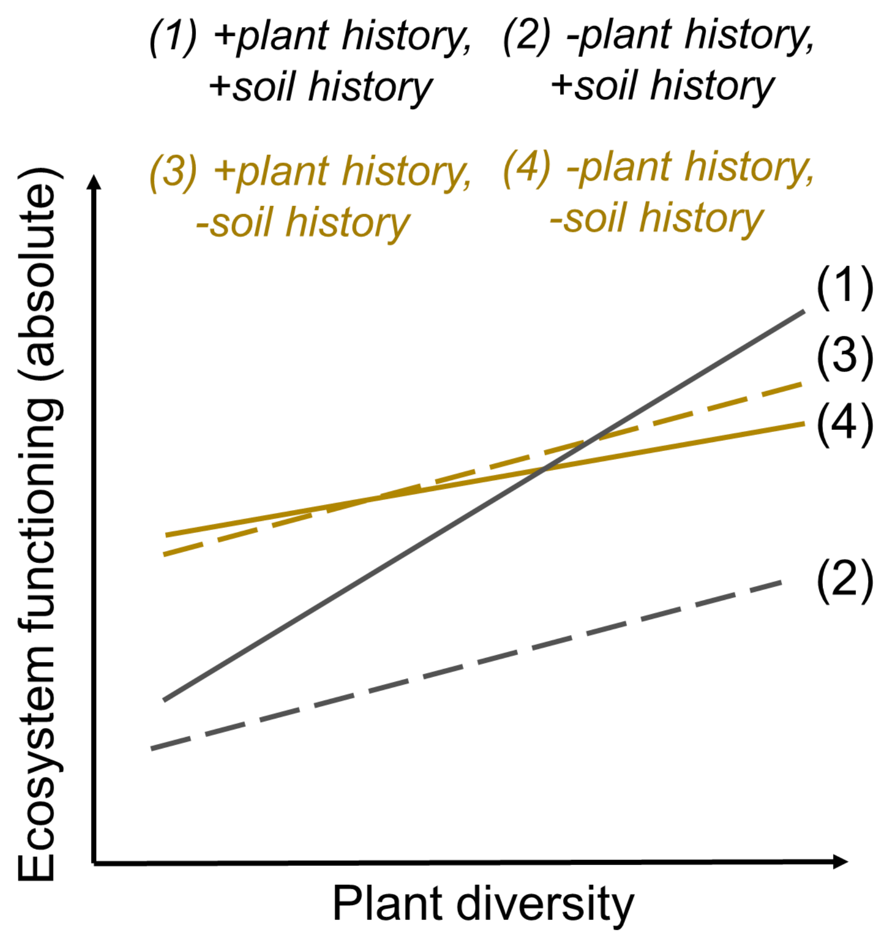
Cheat Sheet
The Ecotron Experiment

Rationale & Hypothesis

This experimental setup allows us to test the independent and interactive effects of plant history and soil history on ecological communities and functions using an orthogonal cross of these treatments

We expect to observe the steepest and most significant BEF relationship in the treatment '*with plant history, with soil history*' and the weakest relationship '*without plant history, without soil history*'



Experimental Setup

Four treatments will be established in the iDiv Ecotron by excavating monoliths from the Trait-Based Experiment and long-term bare ground plots

(1) With plant history, with soil history (Main Experiment):

- Soil communities of 11-year old plots of the TBE
- Seeds from plants with plot-specific history collected in the TBE

(2) Without plant history, with soil history:

- Removal of the established plant communities (upper 5 cm of soil were removed); underlying soil will be kept
- Establishment of new plant communities (sowing of seeds that were used to plant the TBE in 2010)

(3) With plant history, without soil history:

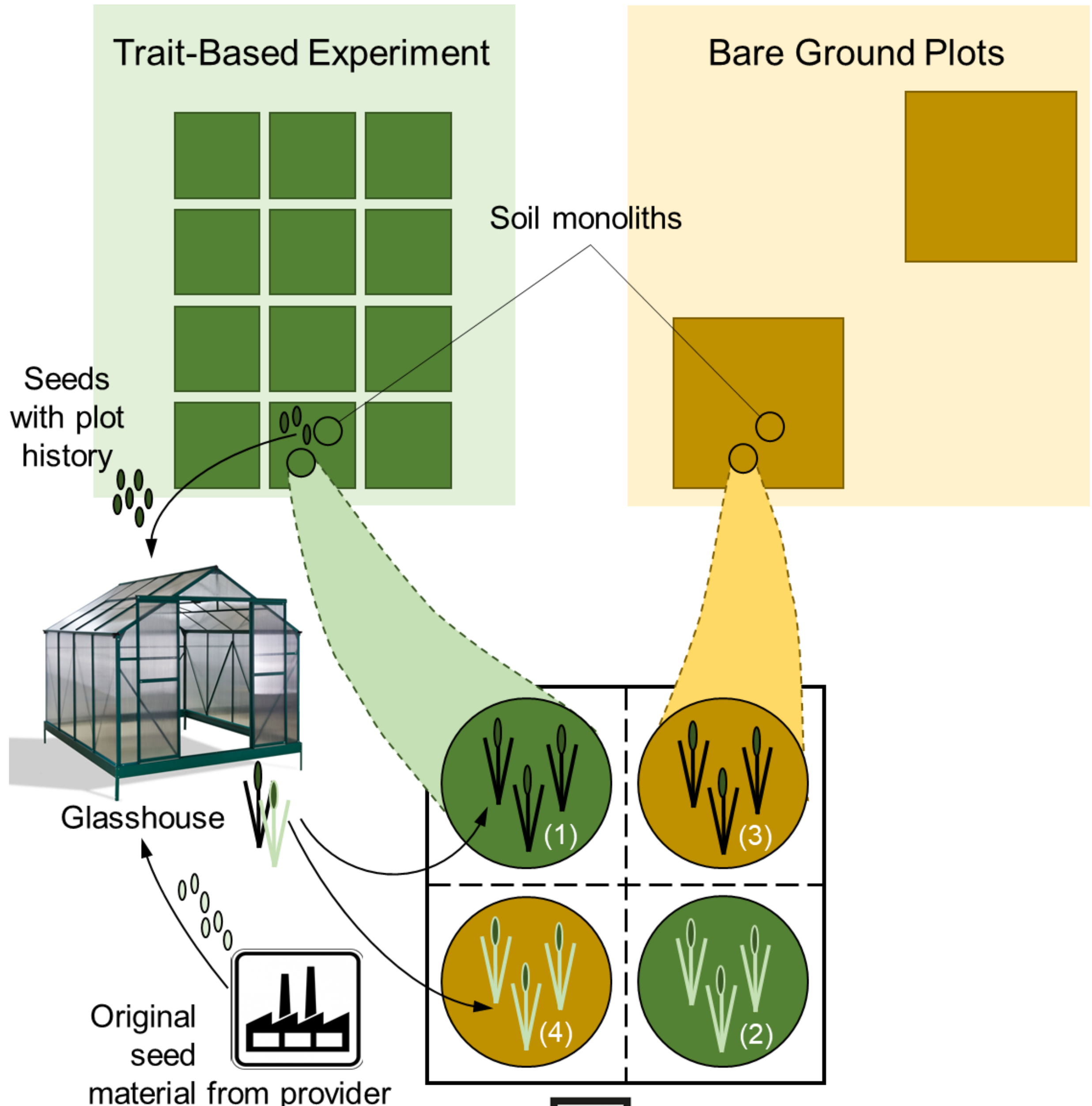
- Soil from bare ground plots without plant-specific history
- Seeds from plants with plot-specific history

(4) Without plant history, without soil history:

- Soil from bare ground plots without plant-specific history
- Establishment of new plant communities (sowing of seeds that were used to plant the TBE in 2010)

Plot Design

- Twenty-four plots of the TBE were selected to cover a plant diversity gradient of 1, 2, and 3 species (plus two plots with 6 plant species as high-diversity control)
- The plant communities also differ in the diversity and dissimilarity of temporal plant resource acquisition traits
- One unit of the Ecotron will harbor four separated monoliths, two with plot-specific soil history (from the same TBE plot) and two without soil history (from the bare ground plots) (24 units, 96 monoliths in total)
- Investigations will be performed at the community- and the species level. The different subprojects will sample plots in concerted actions using joint sampling campaigns and sharing samples (soils, plants). Species-level analyses will be performed using planted phytometers and selected resident plants.



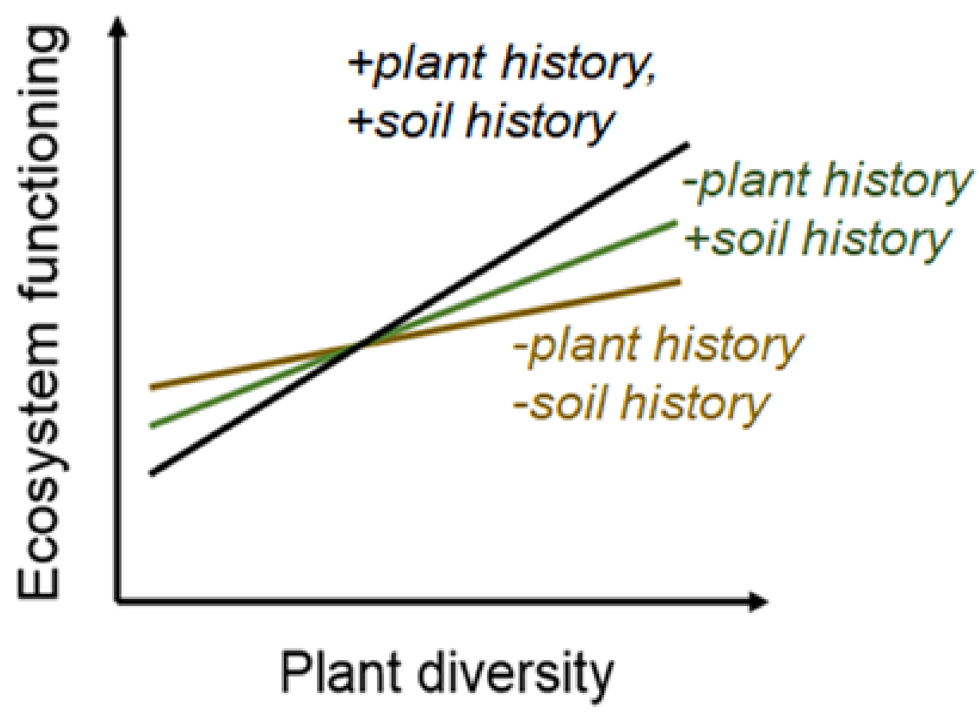
ecotron

Cheat Sheet
The Field Experiment

Rationale & Hypothesis

This experimental setup allows us to test the role of soil biota (plant antagonists and plant growth facilitators) and plant community assembly for changing BEF relationship over time by controlling for effects of calendar year

We expect to observe the steepest and most significant BEF relationship in the treatment ‘*with plant history, with soil history*’ and the weakest relationship ‘*without plant history, without soil history*’



Experimental Setup

Building on the 80 plots of the Main Experiment set up in 2002, three treatments (=subplots; 240 subplots in total) were established per plot:

(1) With plant history, with soil history (Main Experiment; since 2002):
- 17-year old plots with established plant- and soil communities
- No disturbance; serve as control

(2) Without plant history, with soil history (established in 2016):
- Removal of the established plant communities (upper 5 cm of soil were removed)
- Homogenization of the underlying, established soil community to a depth of 30 cm
- Establishment of new plant communities (sowing of seeds from commercial supplier), according to the initial design of the Main Experiment

(3) Without plant history, without soil history (established in 2016):
- Removal of the established plant and soil communities communities (upper 30 cm of soil were removed)
- Exchange by soil from an adjacent agricultural field site without soil history
- Establishment of new plant communities (sowing of seeds from commercial supplier), according to the initial design of the Main Experiment

Earthwork in May 2016

Established plots in June 2016

Plot Design

- 240 subplots were established in 80 plots
- Treatments are randomly located across plots
- Soil nutrients and seed banks were not manipulated, but are measured to account for potential differences when comparing data for the 1- or 2-year-old new communities (2017, 2018, and so on) with data collected in years 2003, 2004, and so on for the now old communities
- Investigations will be performed at the community- and the species level. The different subprojects will sample plots in concerted actions using joint sampling campaigns and sharing samples (soils, plants). Species-level analyses will be performed using planted phytometers and selected resident plants

Location of subplots in exemplary plot